The Function of the Four Types of Waving Display in Uca lactea: Effects of Audience, Sand Structure, and Body Size

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The function of the four types of waving display in *Uca lactea*: Effects of audience, sand structure, and body size

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Four types of claw-waving display in the fiddler crab *Uca lactea*

(4200 words)

ABSTRACT

Multiple signals that convey different messages have been reported in many taxa, but relatively few studies have been made on such signals in invertebrates. In the present study, I investigated four types of claw-waving display used in the fiddler crab *Uca lactea* to test whether the displays have different functions. Three males with a sand structure beside their burrows (which can attract females) and three males without a sand structure were fenced in an opaque enclosure, and I videotaped their waving displays after releasing two burrowless males or two burrowless females to test the effects of audiences. (a) Lateral-circular waving tended to occur in enclosures with burrowless females and was performed frequently by males that had sand structures. (b) Lateral-flick waving was performed frequently by males without sand structures, and its frequency was positively correlated with the signaler's body size. (c) Rapid-vertical waving was observed frequently in enclosures with burrowless males, and its frequency was negatively correlated with the signaler's body size. (d) Circular waving tended to occur in enclosures with burrowless females and was performed frequently by males that had sand structures, and its frequency was positively correlated with the signaler's body size. In my previous study, lateral-circular waving was often seen in the breeding season and was mostly performed to female audiences, lateral-flick waving was frequently performed to neighboring resident males, rapid-vertical waving was performed mainly to intruding burrowless males, and circular waving did not have apparent audiences in most cases. Finally, I concluded that lateral-circular waving was used as a courtship display, lateral-flick waving was related to border disputes, rapid-vertical waving was used for burrow guarding, and circular waving was used to broadcast the signaler's general quality.

Key words: multiple signals; claw-waving display; fiddler crab; *Uca lactea*

INTRODUCTION

Animals in a broad range of taxonomic groups are known to use several distinct signals within a species (Narins & Capranica 1976; Borgia 1995; Zuberbuhler 2000; Coleman et al. 2004; Elias et al. 2005; Hegyi et al. 2007; How et al. 2007; Bro-Jorgensen & Dabelsteen 2008; Chaine & Lyon 2008). A number of hypotheses have been proposed to explain why animals

use multiple signals rather than just one (reviewed in Candolin 2003; Hebets & Papaj 2005; Bro-Jorgensen 2010). One intuitive explanation is that several signals are used to convey different messages (e.g., Zuberbuhler 2000; Candolin 2003; Chaine & Lyon 2008). For example, sexual signals to mates and agonistic signals to rivals may be used to provide different information: sexual signals convey information about heritable genetic quality that contributes to offspring viability or attractiveness, and agonistic signals convey information about the signaler's current fighting ability (Bro-Jorgensen 2010).

In a previous study, I observed a natural population of the fiddler crab *Uca lactea* and found that males perform four distinct types of claw-waving display: lateral-circular, lateral-flick, rapid-vertical, and circular waving (see Muramatsu 2011 for behavioral descriptions). These displays may convey different messages, because the major audience and the seasonal occurrence patterns of the displays differed among waving types (Muramatsu 2011). I predicted that lateral-circular waving was used for courtship because this waving was often seen in the breeding season and was mostly performed to female audiences; lateral-flick waving was used in border disputes because this waving was frequently performed to neighboring resident males; and rapid-vertical waving was used for burrow guarding because this waving was performed mainly to intruding burrowless males. Unlike these types of claw waving it was difficult to deduce the function of circular waving because this waving did not have obvious audiences in most cases. In the previous study, I predicted the functions of displays based on the audiences; however, the density of crabs and the sex ratio are not very stable during the crabs' active season (Muramatsu 2010a) and thus the encounter rate between signaler and some specific audiences may differ depending on the observation date. In the present study, I performed field experiments using an opaque enclosure to manipulate the density and sex of the audience around the signaler.

Each day, I removed all crabs except for six males from the enclosure, and then I released two burrowless males or females in the enclosure in order to observe their claw-waving in the presence of different audiences. I expected that courtship displays would be performed frequently in the enclosures with burrowless females, and that agonistic displays would be performed frequently in enclosures with burrowless males. Additionally, I examined the effects of the signaler's body size and the possession of a sand structure at the burrow entrance to test whether the male’s condition affects his claw-waving. A sand structure is a type of courtship signal which helps to entice females into the

burrow (Christy 1988a; Christy et al. 2003a, b). Several authors have suggested that the possession of a structure is costly for burrow residents (Backwell et al. 1995; Christy 1988a; Muramatsu 2009) and thus males that build structures may be in good condition (Backwell et al. 1995; Muramatsu 2010a). I predicted that males with a structure would perform courtship display more frequently than males without a structure because well-conditioned males would be capable of investing more time and energy in reproductive behavior.

METHODS

The study site was located at a dense colony of *U. lactea*, which was approximately 3500 m² in area, centered on an intertidal mudflat in the estuary of the Yabusa River, Kagoshima, Japan (31º 41' N, 130º 17' E). Crabs emerged from their burrows and were active on the mudflat surface during diurnal low tides, and approximately 45% of males constructed a sand structure at the entrance to their burrows (Muramatsu 2010b). In addition to these resident crabs, there were also some burrowless crabs (crabs that did not have their own burrow) wandering on the mudflat. All observations and experiments were conducted during spring tides in the breeding season, from June to August 2005, except on the days with heavy rain.

Each day, a wooden enclosure (50 × 50 cm², 7 cm high) was placed on the mudflat to fence in three males with a structure and three males without a structure. The enclosure was high enough so that the crabs were visually and physically isolated from the rest of the population. Crabs other than these six males were removed from the enclosure and their burrows were covered with soil to obliterate the entrances. In cases where the sand structures were constructed or destroyed, or irrelevant crabs emerged from the mudflat during the observation, the data were discarded.

To record the claw-waving of the males, the area within the enclosure was videotaped using a SONY DCR-TRV900 digital video camera on a tripod. Just before I started videotaping, I captured two burrowless males or two burrowless females at the study site and released them in the enclosure to investigate the effects of the audience on the frequency of claw-waving. Therefore, each enclosure holds either a pair of burrowless females or a pair of burrowless males. I started videotaping at the time of lowest tide, but the first 10 minutes were not used and next 10 minutes were used for data analyses

because camera-setting inevitably disturbed crab behavior. After videotaping, the crabs in the enclosure were captured, sized, and marked with paint marker in order to avoid duplication. Crabs were captured by blocking the way back to their burrows using a wooden stick (see Muramatsu 2010a for details), and their carapace width was measured with calipers to the nearest 0.05 mm. These videotaped spots were marked with 1-m-long, 4-mm-diameter wooden poles, which were inserted vertically into the sediment, leaving approximately 5 cm above the surface. The area surrounding the pole (approximately 3 m radius) was not used again.

Males of *U. lactea* perform four types of claw-waving: lateral-circular, lateral-flick, rapid-vertical, and circular waving (see Supporting Information 1, 2, 3, and 4, respectively). To count the strokes of each claw-waving on the video footage, I used the following criteria:

(a) Lateral-circular waving (combinations of slow lateral extension, quick flexion, and circumduction of the large claw): I count each quick flexion as one stroke.

(b) Lateral-flick waving (quick lateral abduction to the audience): I count each lateral whip motion as one stroke.

(c) Rapid-vertical waving (rapid dorso-ventral protraction and retraction): I count each upward motion as one stroke.

(d) Circular waving (simple circumduction): I count each full circular motion as one stroke.

I treated the stroke number during the observation (10 minutes) as the frequency of claw-waving display. Note that waving frequency are not directory comparable among waving types because the time and energy required for one stroke would be different. Some types of waving tend to be performed at the entrance to the signaler's burrow. Therefore I recorded whether the signaler was in contact with the burrow entrance when they perform claw-waving.

The four types of claw-waving were separately counted and the effects of body size (carapace width of a focal male), sand structure (present or absent), and wanderers (burrowless males or females) on the frequency of each type of claw-waving were analyzed using glmmML (Generalized linear models with random intercepts; Broström 2009) implemented in the statistical package R (R Development Core Team 2009). This glmmML function fits the model using maximum likelihood and numerical integration via the Gauss-Hermite quadrature. The Poisson distribution with log link function was used to run count regression with each enclosure used as a random factor, and Akaike's Information Criterion (AIC; see Akaike 1974) was used for model

selection. I calculated AIC values for all possible models with or without the explanatory variables, and the model that yielded the smallest AIC value was selected as the best model to predict the frequency of claw-waving.

RESULTS

A total of 16 males in the five enclosures with burrowless females and 12 males in four enclosures with burrowless males were captured after they had been videotaped. The average carapace width was 14.14 ± 0.27 mm (mean ± SE) in males that had sand structures and 14.37 ± 0.19 mm in males that did not have a structure.

(a) Lateral-circular waving

The best model for lateral-circular waving had presence of sand structure and sex of wanderer as explanatory variables (Table 1a, top row). Males that had structures performed this waving more frequently than males that did not have structures, and males with burrowless females performed this waving more frequently than males with burrowless males (Fig.1a; Table 1a, top row).

(b) Lateral-flick waving

The best model for lateral-flick waving had body size and presence of sand structure as explanatory variables (Table 1b, top row). The waving frequency of focal males was positively correlated with their body size, and males that did not have a structure performed this waving more frequently than males that had structures (Fig. 1b; Table 1b, top row).

No males performed lateral-flick waving at the entrance to their burrows (Table 2).

(c) Rapid-vertical waving

The best model for rapid-vertical waving had body size and sex of wanderer as explanatory variables (Table 1c, top row). The waving frequency of focal males was negatively correlated with their body size, and males with burrowless males performed this waving more frequently than males with burrowless females (Fig 1c; Table 1c, top row).

Compared to the three other types of waving, rapid-vertical waving tended to be performed at the entrance to the signalers' burrows (Table 2).

(d) Circular waving

The best model for circular waving had body size, presence of sand structure, and sex of wanderer as explanatory variables (Table 1d). The waving frequency of focal males was positively correlated with their body size. Males that had structures performed this waving more frequently than males that did not have structures, and males with burrowless females performed this waving more frequently than males with burrowless males (Fig. 1d; Table 1d, top row).

DISCUSSION

Claw-waving of fiddler crabs has often been explained as a signal used in courtship (e.g., Yamaguchi 1983, 2001; Burford et al. 2000; Pope 2000a, b; Christy et al. 2001, 2002) and/or aggression (e.g., Crane 1958; Salmon 1965; Zeil et al. 2006). Unlike other fiddler crab species, however, males of *Uca lactea* perform four distinct types of claw-waving display (Muramatsu 2011). Therefore, the four types of waving in *U. lactea* may have more specific functions other than the general categories of courtship and aggression.

In my previous study, I predicted that lateral-circular waving would be used for courtship, because this waving was mostly performed to female audiences and was observed frequently in the breeding season (Muramatsu 2011). Additional data obtained in the present study showed that males in enclosures with burrowless females performed this waving more frequently than males with burrowless males, and males that had sand structures performed this waving more frequently than males without structures (Fig. 1a, Table 1a). Both results are consistent with the prediction that lateral-circular waving is related to courtship behavior.

By contrast, lateral-flick waving may be an offensive territorial display, which is used in border disputes against neighboring resident crabs. This waving is frequently performed to both sexes of neighbor residents but is rarely performed to resident females in the breeding season (Muramatsu 2011). In *U. lactea*, resident females can be the rivals for males in border disputes, because residents of both sexes defend their territories around their burrows (Yamaguchi & Tabata 2004). In the breeding season, however, a resident female can also be a mating partner (Goshima & Murai 1988; Yamaguchi 2001) and perhaps aggressive territorial displays would be suppressed in this period. In the present

study, the frequency of lateral-flick waving was positively correlated with the signaler's body size (Table 1b), suggesting that larger males were more aggressive than smaller males. Meanwhile, males with sand structures performed lateral-flick waving less frequently than males without structures (Table 1b), possibly because the territories around burrows without sand structures were more likely to be intruded into by other crabs and consequently the burrow residents had to perform this waving frequently. Indeed, in the absence of predators, burrows without sand structures were more frequently visited by burrowless males than those with sand structures (Muramatsu, unpublished data). This difference in the probability of approach could help to explain why some studies have suggested that sand structures reduce aggressive behaviors among resident males (Zucker 1974, 1981; but see Christy 1988b).

Rapid-vertical waving may also be used as a territorial signal, but this waving appeared to be used more defensively than lateral-flick waving. Rapid-vertical waving was frequently performed at the entrances to the signalers' burrow while no males perform lateral-flick waving at the burrow entrances (Table 2) perhaps because rapid-vertical waving was used for burrow guarding but not for border disputes. Because there are many burrowless crabs in the field either looking for an empty burrow or attempting to take over a burrow from other crabs (Pope 2005; Zeil et al. 2006), resident crabs may need to defend their burrows from intruding crabs. Presumably, resident crabs are able to deter intruders by performing this waving when they detect intruding crabs, because it would be difficult for intruders to steal a burrow from residents when the residents are aware of the intruder. It is noteworthy that the frequency of rapid-vertical waving was negatively correlated with the signaler's body size (Table 1c) and resident females also showed a similar claw-waving with their small claws. This waving may not therefore be used to convey the signaler's fighting ability or an aggressive message, but to show the signaler's awareness of intruding burrowless crabs. In the present study, as expected, males with burrowless males in an enclosure performed rapid-vertical waving more frequently than the males with burrowless females (Table 1c). Although some males performed this waving to burrowless females (Fig. 1c), most males switched their display to lateral-circular waving when the burrowless females got closer. Perhaps any burrowless crabs initially elicit precautionary behavior of resident crabs until the residents recognize the sex of the intruder.

The most puzzling display of *U. lactea* is circular waving. Circular

277 waving does not have an apparent audience in most cases and is frequently
278 observed prior to the breeding season (Muramatsu 2011). Likewise, some
279 species of fiddler crabs perform claw-waving in the absence of any specific
280 audience (Crane 1958; Christy et al. 2001; How et al. 2008) and these
281 spontaneous displays may act as "broadcast" signals that are performed to a
282 number of unspecified potential audiences (see Martins 1993; How et al. 2008).
283 The results of the present study showed that the frequency of circular waving
284 was positively correlated with the signaler's body size, and males with sand
285 structures performed this waving more frequently than males without structures
286 (Table 1d). Because both large body size and the possession of a structure are
287 expected to be related to male quality, circular waving may be used to
288 broadcast the signaler's general quality. In the present study, males with
289 burrowless females performed circular waving more frequently than males with
290 burrowless males (Table 1d), suggesting that the presence of burrowless
291 females elicited circular waving more strongly. Hence, the baseline audience of
292 this waving might be females, even though this waving does not seem to be
293 directed to them. Given that circular waving was directed to females, this
294 waving could be similar to lateral-circular waving. In my previous study,
295 however, circular waving was most frequently performed prior to the breeding
296 season, whereas lateral-circular waving was most frequently performed in the
297 breeding season. Alternatively, circular waving in the present study might have
298 been elicited by other males' waving. Males of *U. mjoebergi* are known to
299 eavesdrop on the waving displays of nearby males (see Milner et al. 2010). In
300 the present study, males in the enclosures with females may have performed
301 circular waving frequently (Fig. 1d) because nearby males often showed lateral-
302 circular waving toward burrowless females (Fig. 1a).
303 In conclusion, the results showed that lateral-circular waving may be
304 used as a courtship display to attract females, lateral-flick waving may be an
305 offensive territorial display relating border disputes, rapid-vertical waving may
306 be a defensive territorial display used for burrow guarding, and circular waving
307 may be a kind of broadcast signal to show the signaler's general quality.
308 Although further investigation on the response of audiences may be needed to
309 confirm that these four types of claw-waving are related to distinct functions, it
310 is clear that males of *U. lactea* use four types of claw-waving display in different
311 contexts. This kind of complex signaling may also be employed in other
312 invertebrate taxa, especially in group-living species that form mixed-sex
313 colonies.

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474 **TABLE**

475 Table 1: Parameter estimates and AIC values in GLMMs for each waving.

476

AIC	parameter estimate±SE			
	intercept	body size	sand structure (absent)	wanderer (male)
(a) Lateral-circular waving				
132.1	1.833±0.496	-	-1.855±0.406	-4.322±1.271
133.7	2.710±1.495	-0.062±0.099	-1.903±0.414	-4.308±1.268
141.4	0.121±0.879	-	-1.867±0.406	-
143.0	1.021±1.676	-0.063±0.100	-1.917±0.414	-
161.1	1.602±0.517	-	-	-4.509±1.299
162.6	0.643±1.400	0.067±0.091	-	-4.530±1.306
170.9	-0.207±0.918	-	-	-
172.3	-1.209±1.611	0.069±0.091	-	-
(b) Lateral-flick waving				
113.4	-4.099±2.286	0.246±0.151	0.597±0.287	-
114.2	-0.601±0.728	-	0.710±0.281	-
114.5	-4.580±2.386	0.244±0.152	0.594±0.286	1.110±1.203
115.2	-1.115±0.969	-	0.706±0.280	1.139±1.185
115.8	-5.020±2.321	0.318±0.151	-	-
116.9	-5.567±2.434	0.317±0.151	-	1.242±1.328
118.7	-0.440±0.812	-	-	-
119.7	-1.019±1.077	-	-	1.290±1.318
(c) Rapid-vertical waving				
1532	9.554±0.454	-0.380±0.019	-	1.038±0.552
1533	10.008±0.420	-0.379±0.019	-	-
1533	9.548±0.456	-0.378±0.019	-0.047±0.036	1.044±0.554
1534	10.006±0.421	-0.378±0.019	-0.047±0.036	-
1980	4.637±0.318	-	-0.078±0.034	-
1980	4.219±0.372	-	-0.078±0.034	0.943±0.556
1983	4.616±0.315	-	-	-
1983	4.203±0.369	-	-	0.930±0.551

(d) Circular waving

200.1	-8.583±1.179	0.775±0.073	-0.584±0.138	-1.365±0.773
200.9	-9.196±1.158	0.776±0.073	-0.587±0.138	-
217.3	-8.149±1.138	0.738±0.070	-	1.437±0.776
218.4	-8.797±1.119	0.738±0.070	-	-
366.1	2.615±0.448	-	-0.511±0.132	-1.289±0.704
367.2	2.046±0.406	-	-0.514±0.132	-
379.8	2.523±0.452	-	-	-1.354±0.711
381.1	1.922±0.414	-	-	-

FIGURE LEGENDS

Fig. 1: The frequency of waving in different conditions.
"wanderer" indicates the type of burrowless audience (females or males) in the enclosure. "sand structure" indicates the possession of a sand structure (present or absent).

Fig. 2: The proportion of waving performed at the burrow entrance.

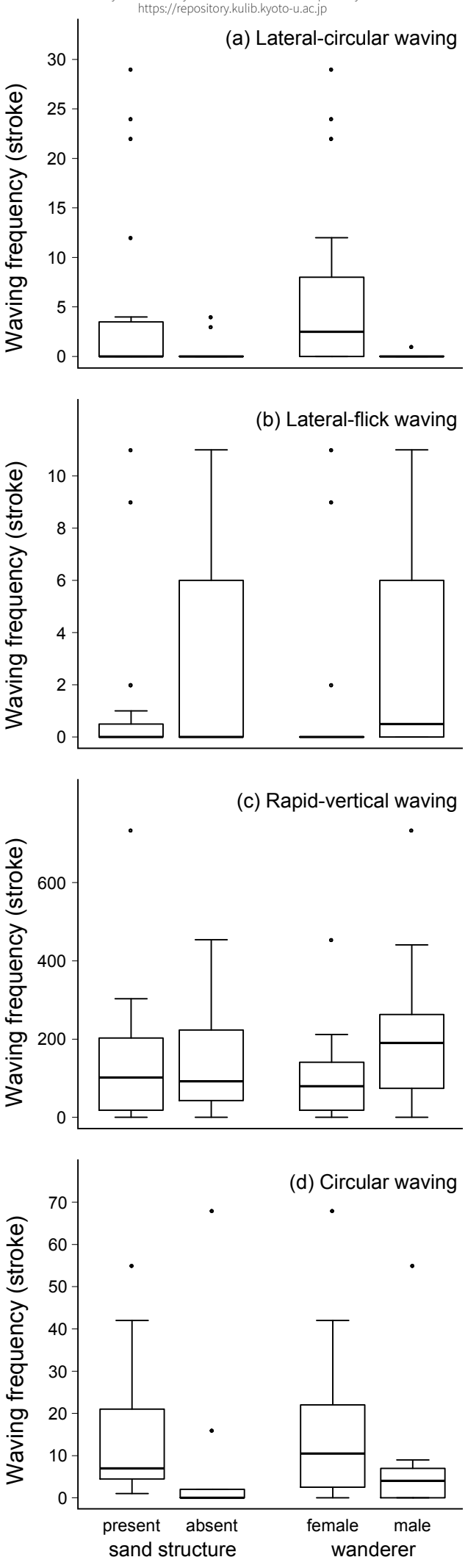

Fig. 1

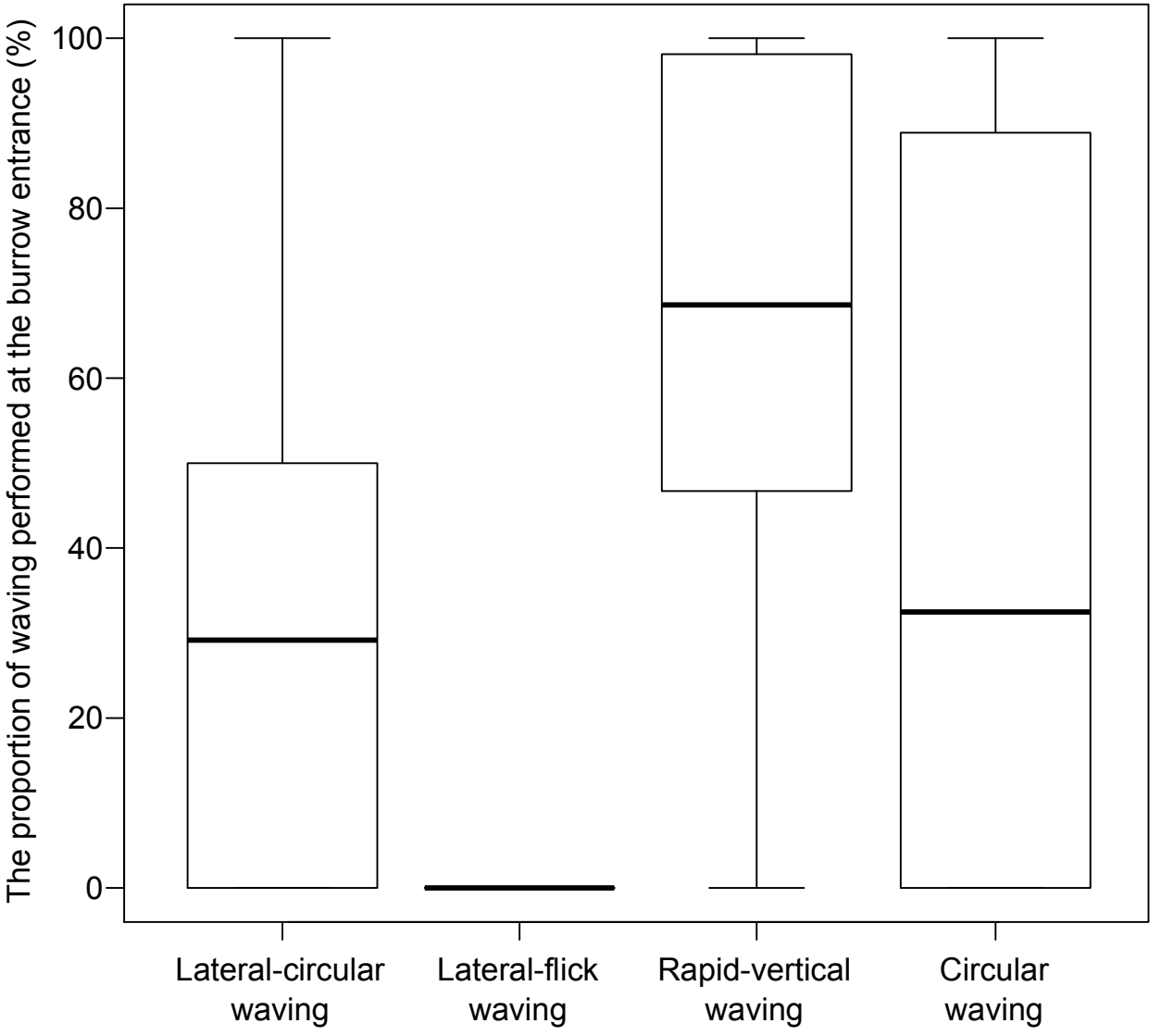

Fig. 2